

Axial myology of the Racer *Coluber constrictor* with emphasis on the neck region

Gregory K. Pregill

ABSTRACT.—Little is known about the evolution of the occipito-vertebral joint in limbless vertebrates and how the neck has been affected by the loss of a shoulder girdle. Snakes are perhaps the most specialized limbless vertebrates. The neck region of *Coluber constrictor*, an advanced species, is described. An account of the cervical skeleton describes features of the occipito-vertebral joint and the bony elements that are associated with muscles of the anterior trunk. A description of the neck myology follows to (1) explain the change in relationship of the various trunk muscles as they approach the head and (2) state precisely which muscles insert on the skull and how each facilitates cranial mobility. *M. obliquus capitus magnus* and *M. rectus capitus anterior* are prime movers in head flexion and extension and have no trunk counterparts. They are described for the first time in snakes. The neck muscles of *Coluber constrictor* then are compared among several related genera to assess variation. Finally, the major features of neck morphology are analyzed. Evolutionary implications are discussed and a comparative study with other snakes and lizards is proposed.

In the evolution of land vertebrates the cranial-atlas-axis complex and its associated musculature has played an important role in facilitating cranial mobility. The transformation of the generalized first vertebra into the atlas in early amphibians provided an occipito-vertebral articulation that permitted vertical or horizontal movement of the head independent of the trunk. Subsequent specialization in the reptiles of the second vertebra as the axis allowed rotation of the head. Still greater freedom of movement was effected by a reduction in the number of freely articulating ribs on those vertebrae immediately behind the axis. The general pattern of evolution of these skeletal elements and their associated muscles now is well known, but there remain a number of curious specializations in the cervical region that are not yet fully understood. Among the departures from the usual plan are those amphibians and reptiles in which the limbs and girdles have become reduced or lost entirely.

Cranial mobility in tetrapods is a response to an increased horizon resulting from an elevated body, but in limbless vertebrates such as snakes the body is flush with the substrate so that head mobility must be adapted not only for orientation within the environment but for other functions as well—feeding, climbing and burrowing, for example. In snakes the structural significance of the occipito-vertebral region is not easily recognized because the shoulder girdle has been lost and the vertebral skeleton and its associated muscles have become dedifferentiated. That is, the neck and trunk are no longer structurally and functionally independent. For example, the muscles of the neck have either joined with or been replaced by the long muscles of the trunk. The effect of this change on cranial mobility is unknown. The significance of the neck region in the evolutionary transition is obvious, but on the whole it has been ignored in previous studies on snake morphology.

It has been inferred erroneously from the studies on the trunk myology of snakes by Nishi (1916) and Mosaur (1935) that the neck is simply the most anterior portion of the trunk which abruptly terminates (or begins) at the head. Neither Nishi nor Mosaur included the cervical region in their analyses. Although

more recent papers by Auffenberg (1958, 1961, 1962, 1966), Gasc (1967) and Ludicke (1962) have renewed interest in snake myology, their work pertains to the trunk and does not include study of the neck region. In this paper I have attempted to ascertain the effect of the absence of an appendicular skeleton on the neck morphology in a colubrid snake. Although the emphasis is descriptive, functional properties are discussed where appropriate.

The classification of higher snakes (caenophidians) is unstable and in particular, the composition of the family Colubridae has undergone extreme changes in recent years (see Bailey, 1967; Dessauer, 1967; Dowling, 1967; Rossman, 1967; Underwood, 1967a). In its most restricted sense the family is composed of advanced snakes having the following characters: asymmetrical hemipenes; a simple sulcus spermaticus passing over to the left hand side of the hemipenis; a simplex retina; a vidian canal that generally is short; and a levator anguli oris muscle that usually is absent (Underwood, 1967b). In following Underwood's classification I am not arguing the higher taxonomic categories of snakes, but only informing the morphologist as to the identity of the animal studied. Thus, *Coluber constrictor* was chosen because (1) throughout all taxonomic rearrangements the species always has been considered among the most advanced species of snakes, (2) the overall anatomy of the genus is known fairly well, (3) an adequate sample of preserved specimens was available for dissection, and (4) the genus serves as the type of the family.

MATERIALS AND METHODS

This study is based on dissection of the trunk and neck muscles of forty preserved snakes. There were twenty *Coluber constrictor mormon* (Baird and Girard) representing 11 adults and nine sub-adults and juveniles of both sexes. Adults of five other colubrid genera and one natricid genus dissected for comparison included: *Lampropeltis getulus californiae* (4), *Elaphe g. gutta* (3), *Drymarchon corais erebennus* (3), *Pituophis melanoleucus annectens* (1), *Chionactis occipitalis annulata* (3). Natricidae: *Thamnophis sirtalis* (6).

Dissections were made with the aid of a binocular microscope. At the beginning of the study a few specimens of *Coluber* were completely dissected individually. Once a technique was established specific muscles of several snakes could be examined simultaneously. Skeletal material of each species was at hand to facilitate the location of muscle origin and insertion and to aid in osteological description.

The illustrations accompanying the text depict muscles as they were exposed, but by necessity the figures are semi-diagrammatic to emphasize important topographical relationships. The muscle descriptions define the adult, but include pertinent comments on juveniles. The juvenile condition and subsequent ontogeny is summarized in the discussion at the end of the paper. The terminology of the trunk musculature is from Mosaur (1935), the facial muscles from Haas (1973), and names of certain occipito-vertebral muscles are my own.

OSTEOLOGY OF THE NECK REGION

Attention to neck osteology is focused on two areas—the occiput and the anterior vertebral column. Together with the muscles these bones produce movement of the head independent from the rest of the body and make up the vaguely defined neck of the snake. The occipital region of the skull is relatively simple and will be discussed in a later section. The vertebral column is more complex. There is no differentiated cervical region. Furthermore, the whole vertebral column lacks the regionalization characterizing higher tetrapods, which possess distinct cervi-

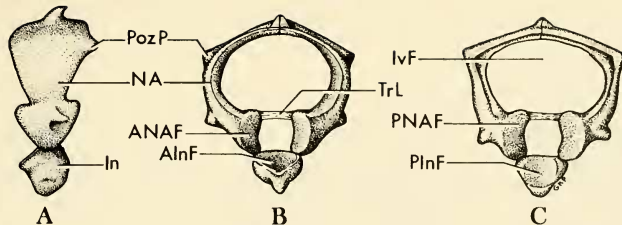


Figure 1. Atlas, *Coluber constrictor*: A, lateral; B, anterior; C, posterior. AlnF, anterior intercentral facet; ANAF, anterior neural arch facet; In, intercentrum; IvF, intervertebral foramen; NA, neural arch; PlnF, posterior intercentral facet; PNAF, posterior neural arch facet; PozP, postzygapophyseal process; TrL, transverse ligament.

cal, thoracic, lumbar, sacral and caudal regions. Snake vertebrae traditionally are viewed as either "presacral" or "caudal." Although there have been many attempts to define cervical vertebrae only the atlas and axis are distinctive. The study of snake osteology has a lengthy history and the current knowledge of the subject is summarized by Hoffstetter and Gasc (1973).

The vertebral column of snakes is unique among limbless vertebrates and eludes stereotyping. For example, between successive vertebrae there are five points of articulation instead of three and the column functions more as a cable than a hinge (Auffenberg, 1962). Johnson (1955) concluded from a statistical survey on vertebral morphology in snakes that vertebral structure is conservative, varying minimally across major phyletic lines, despite extreme variation in adaptive modes within these lines. His conclusions are consistent with Mosaur's (1935) findings on trunk muscles. So it is not surprising that almost any description of snake vertebrae, regardless of species, is fairly applicable to any other. For example, the description by Williams (1959) of the occipito-vertebral joint in *Cylindrophis rufus*, an oriental burrowing snake, could be used for *Coluber*.

The morphology of snake vertebrae is further characterized by a reduction in surface area available for muscle attachment. Muscles originate and insert on structures such as hypapophyses, neural spines and accessory processes on the zygaophyses. These structures are present in the neck, but differ on each of the first three vertebrae. The atlas, axis and anterior trunk vertebrae of *Coluber constrictor* are described briefly below as they relate to each other and with the skull.

Atlas.—The first vertebra, or atlas, is a more or less ring-shaped structure consisting of three bones (Fig. 1). Laterally and dorsally are two thin neural arches loosely sutured to each other mid-dorsally. Ventrally the ring is completed by the single intercentrum ligamentously attached to the pedicel of each neural arch. Each neural arch bears large elliptical facets on the anterior and posterior surface of the pedicel that articulate with the occipital condyle in front and the axis behind. On the lateral surface of each pedicel is a short median transverse process. A second process projects from the dorsolateral angle of the arch as a small conical protuberance analogous to the postzygapophyseal process of the trunk vertebrae. From their pedicels the arches curve dorsally and become wider in the anteroposterior plane. The arches meet at the dorsal midline to enclose the intervertebral foramen (neural canal). There is no neural spine dorsally, but a small midsagittal crest instead.

The atlas intercentrum is a single midventral element bearing articular facets on its anterior and posterior surfaces similar to those on the arch pedicels. A basal prominence, or hypapophysis, is present, but it is much smaller than the hypapophyses of other vertebrae.

With the three bones joined in a ring, the anterior face of the atlas forms a midventral cotyle for the reception of the occipital condyle. The posterior face mirrors the anterior face and forms a concavity that receives the odontoid process of the axis. The two concavities complete a canal, or foramen septi, which is

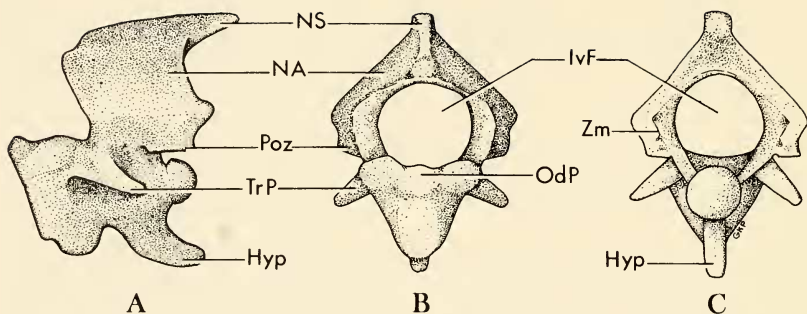


Figure 2. Axis, *Coluber constrictor*: A, lateral; B, anterior; C, posterior. Hyp, hypapophysis; IvF, intervertebral foramen; NA, neural arch; NS, neural spine; OdP, odontoid process; Poz, postzygapophysis; TrP, transverse process; Zm, zyganchrum.

separated from the intervertebral foramen above it by the ligamentum transversum (transverse ligament). The ligament spans the dorsomedial surface of the arch pedicels.

Axis.—The axis of *Coluber* (Fig. 2) consists of an anterior cone-shaped odontoid process flattened on its dorsal surface; an intercentrum below the odontoid, a median centrum (body) terminating caudally in a ball-like condyle, and a pair of neural arch halves fused middorsally in a strong spinous process. The neural arch bears a pair of postzygapophyses and a weakly developed zyganchrum for articulation with the third vertebra. Two hypapophyses are present on the ventral surface of the axis. The anterior one is a basal outgrowth of the intercentrum. The better developed posterior hypapophysis arises from the centrum and slopes backward.

The axis articulates with the atlas by two lateral facets on the odontoid and by the vertical anterior face of the intercentrum. The odontoid is received by corresponding facets on the atlas neural arch pedicels while the intercentrum fits flush with the opposing face on the atlas intercentrum. The articulation permits little vertical movement, but slightly more rotational and horizontal movement. Moreover, the tip of the odontoid barely makes contact with the depression on the occipital condyle (fovea dentis of Williams, 1959). Thus, articulation between the skull and the vertebral column is primarily by the atlas.

Anterior trunk vertebrae.—The 15 to 20 vertebrae immediately caudal to the axis (Fig. 3) differ little from the others of the trunk. Neural spines, accessory processes and hypapophyses become smaller towards the skull; thus there is a gradual reduction in over-all size of each vertebra so that the column tapers as it approaches the head. Only the third vertebra is at all peculiar. It lacks free ribs but is otherwise only slightly modified in possessing elongate, bilobed parapophyses without articular facets for ribs. Romer (1956) considered these processes to be composed of short fused ribs and hence referred to it as a "cervical" vertebra.

The occiput.—The occipital region of the skull consists of four bones; a dorsal supraoccipital, a pair of lateral exoccipitals and a ventral basioccipital. Only the exoccipitals and basioccipital contribute to the formation of the occipital condyle, but all four serve as sites of attachment for the cervical musculature. Most characteristic are the crest and processes. On the dorsal aspect of the occiput is a prominent transverse crest formed by the median supraoccipital sutured on either side to exoccipitals. The crest rises perpendicular to the roof of the foramen magnum forming a depression for the insertion of the dorsal cervical muscles.

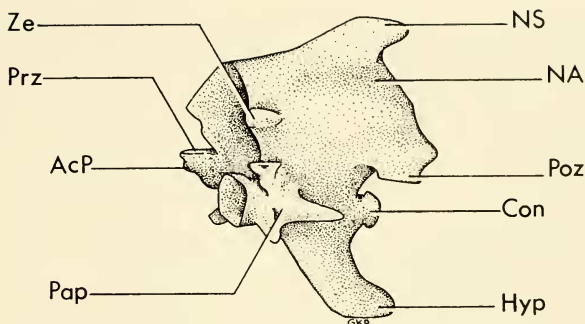


Figure 3. Anterior trunk vertebra, *Coluber constrictor*: Three quarter view, anterior is to the left. AcP, accessory process; Con, condyle; Hyp, hypapophysis; NA, neural arch; NS, neural spine; Pap, parapophysis; Poz, postzygapophysis; Prz, prezygapophysis; Ze, zygosphene.

Laterally the crest of the exoccipitals angles ventrad and caudad becoming smaller as it approaches the basioccipital below. Where these two bones are sutured anterior to the occipital condyle, they form the knob-like paraoccipital process.

The basioccipital forms the ventral plate of the occiput. Posteriorly it terminates as the single median element of the occipital condyle. On its cranial border is a low crest bearing a central, caudally directed process bordered on each side by a small hump. The ventral cervical muscle inserts over the entire surface of the bone. Positions of the crests and processes on the occiput suggest the pattern of insertion for the cervical musculature. These elements are strongest dorsally and ventrally and weakest laterally. Likewise, muscle insertion is mostly dorsal and ventral. Consequently, the occipito-vertebral joint allows more movement in the vertical plane than in the horizontal.

THE MUSCLES

Previous studies on snake myology have been directed toward two broad areas of ophidian biology, namely taxonomy and the evolution of limbless locomotion. These areas, of course, are not mutually exclusive, but express the problems that seemed most obvious to the investigators. The number of such studies exclusive of head musculature is surprisingly few. The more recent and comprehensive of these include papers by Mosaur (1935), Auffenberg (1958, 1961, 1962, 1966), Gasc (1967) and Ludicke (1962).

Mosaur's paper remains the classic. His tripartite classification of snakes based on trunk musculature is basically sound. He recognized little inter-familial variation and concluded that there are three basic types of muscle arrangements, as typified by boids, colubrids and viperids. Auffenberg (1958, 1966) subsequently demonstrated that Mosaur's scheme, although useful as a general application, was over-simplified and of little help in more specific taxonomic problems. Auffenberg examined a number of henophidians (Booids) such as *Eryx*, *Tropidophis*, *Xenopeltis* and *Cylindrophis*. He suggested that the variation observed in the axial spinal muscles indicated certain phyletic tendencies toward the colubrid type of arrangement. He called this "myological colubridization." The fact remains that the colubrid pattern is the most derived. In the Colubridae, certain muscles such as the *M. supracostalis dorsalis* have been lost, whereas others have lost their osseous connections and become associated with adjacent muscles. This is most evident in the fast moving terrestrial racers such as *Coluber*.

In his evolutionary analysis of trunk muscles, Auffenberg (1961) recognized several steps leading to the advanced condition found in racers. He described the events of two major trends that suggest myological evolution from a simpler and presumably more primitive type to the complex or more advanced. These trends are: (1) the tendency for median muscle elements to become associated with more lateral ones and (2) the association of posterior myological elements with anterior ones resulting in lengthening of functional units by the fusion of shorter muscles. This is the most conspicuous feature of colubrid muscles and is most noticeable in the sacrospinalis complex. In most henophidians the *M. spinalis-semispinalis* is a single muscle arising from the neural spine by a tendinous arch. In contrast, the same muscle in colubrids has split posteriorly into lateral and medial elements, each of which arises independently of the other. Moreover, the lateral element arises not from an osseous connection, but instead from the medial tendon of the *M. longissimus dorsi*. Thus, one muscle originates from the terminal tendon of the other, this results in a linkage of separate elements into long myological chains. Furthermore, each chain of elements is overlapped segmentally by similar ones. This myological macramé is significant functionally because it insures uniform and synchronous flexion over long sections of the body.

In the cervical region the trends in myological evolution have occurred concomitant with elongation of the body and loss of the pectoral girdle. Because this paper is concerned with description of the most advanced condition, it is important for the reader to understand that the relationships and arrangements of neck muscles have been obscured by evolutionary change and are not always obvious.

The descriptions that follow are of the muscles of the neck region. Most neck muscles are simply continuations of those of the trunk; however, there are some that are exclusively cervical. Furthermore, many of the trunk muscles have been modified in the neck. For these it will be necessary to first describe them as they appear in the trunk and then describe their modifications in the neck region. Mosaur (1935) has given a thorough account of the trunk myology so I will not provide descriptions as detailed as his. The descriptions given here should give the reader sufficient information to understand the morphological changes that occur in the neck.

Organization of muscle groups.—Organizing the various trunk and neck muscles into meaningful categories is difficult. This is particularly so in colubrid snakes in which the different muscles may be related structurally but not functionally.

Mosaur recognized four main groups of ophidian skeletal muscles; (1) muscles between vertebrae, (2) muscles between vertebra and rib, (3) muscles between ribs and (4) integumentary muscles. This study adds two more groups of muscles—those between the trunk and head, and those muscles continuous with the cervicals but not reaching the head. Of course, several of the muscles may fall into more than one category. For example, the *M. longissimus dorsi* connects articular processes of vertebrae with spinous processes of vertebrae by its medial tendon giving rise to the *M. semi-spinalis*. Its lateral tendon, however, connects articular processes with ribs via the *M. retractor costae biceps*. Table 1 summarizes the main neck muscles inserting on the skull.

The descriptions presented will be organized more or less within Mosaur's categories, but in a different sequence. First will be the cervical muscles themselves (trunk to head) as they are most germane. This group includes the facial muscles and occipito-vertebral muscles. Second will be the modified trunk muscles in the neck region: the axial spinal muscles, subvertebral muscles and other vertebral costal muscles. Third will be the costal muscles and the last category

TABLE 1. Occipito-vertebral muscles of *Coluber constrictor*.

Muscle	Origin	Insertion on occiput	Action
spinalis capitus	neural spines of V2, V3, V4	supraoccipital crest	dorsal extension of head
semispinalis cervicus	anterior medial tendons of longissimus	exoccipital crest	dorsal extension of head and neck
spinalis-semispinalis	2 heads: tendon of multifidus; medial tendon of longissimus	supraoccipital crest	dorsal extension of head and neck
longissimus dorsi	accessory process	exoccipital crest and paraoccipital process	abduction of head and neck
retractor costae biceps	lateral tendon of longissimus	paraoccipital process	abduction of head and neck
obliquus capitus magnus	neural spines of V2, V3, V4	exoccipital	rotation and dorsal extension of head
rectus capitus anterior	hypapophyses of VII to axis	pars ventral: basioccipital pars dorsal: paraoccipital process, basioccipital	ventral flexion of head and neck

includes the miscellaneous muscles elements. The important connective tissue and fascia will be explained following the descriptions of the muscles in *Coluber*.

FACIAL AND OCCIPITO-VERTEBRAL MUSCLES

Facial Muscles.—The four muscles of this group are the Mm. constrictor coli, cervicomandibularis, neurocostomandibularis and retractor quadrati. All insert on the head, but function primarily in feeding and not in cranial mobility. They are considered here because all have their origins on the neck and must be removed to expose the cervical and vertebral muscles that lie beneath them.

The facial muscles have been described for a variety of snake genera. All of the studies that discussed them dealt with jaw mechanics or comparative cephalic anatomy. Haas (1961) discussed the phylogenetic implications of snake head muscles and also provided the most recent complete summary of the subject in Squamata (Haas, 1973). His terminology is employed here except for the M. constrictor coli which he calls the M. sphinctor coli.

M. constrictor coli (Fig. 4): This is the most superficial muscle of the neck region. It is entirely subcutaneous throughout its length and is destroyed easily if the skin is not removed carefully. The M. constrictor coli appears as a wide band or collar just behind the head and is mostly aponeurotic.

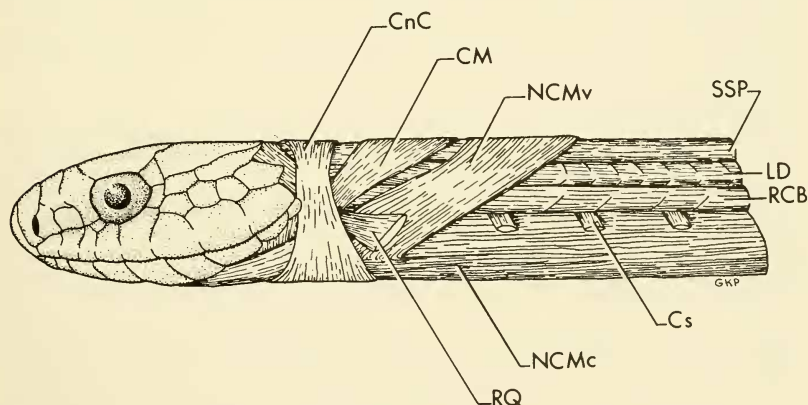


Figure 4. Facial and superficial neck muscles of *Coluber constrictor*: Left lateral view. CM, M. cervicomandibularis; CnC, M. constrictor coli; Cs, M. costocutaneous superior; LD, M. longissimus dorsi; NCMc, M. neurocostomandibularis—costal head; NCMv, M. neurocostomandibularis—vertebral head; RCB, M. retractor costae biceps; RQ, M. retractor quadrati; SSP, M. spinalis-semispinalis.

It originates on the dorsal fascia and runs lateroventrad to insert partly on the hyoid, but principally on the ventral fascia that covers the cartilagenous rib tips. The anterior edge of the muscle barely crosses the posterior corner of the quadrato-mandibular joint. The extent of the posterior edge is variable, but in most individuals it reaches the first or second rib. The muscle has few fibers which are confined to its lateroposterior margin. The fibers extend just past the level of the maxillary ligament.

M. cervicomandibularis (Figs. 4 and 5): Removal of the *M. constrictor coli* exposes two large flat muscles covering the lateral surface of the neck and superficial to all others in the area. The more anterior of these is the *M. cervicomandibularis*. The posterior muscle is the *M. neurocostomandibularis*. The former arises by an aponeurosis from the dorsal fascia between neural spines of the third through fifth vertebrae. Muscle fibers are directed obliquely anteroventrad and converge to form a thin aponeurotic tendon. The tendon inserts on the capsule of the jaw joint. Fibers on the caudal edge may coalesce with the vertebral head of the *M. neurocostomandibularis*, but the two usually can be separated.

M. neurocostomandibularis (Figs. 4 and 5): This large muscle originates on the neck by two widely separated heads and inserts on the mandible by a single head. It arises by a dorsal "vertebral head" and a ventral "costal head." The vertebral head is attached by an aponeurosis to the dorsal fascia that covers the sixth through ninth vertebrae. The muscle fibers sweep downward and cranially as a wide flat sheet somewhat thinner than the *M. cervicomandibularis* which it parallels. The dorsal head of the *M. neurocostomandibularis* inserts on an inscriptional tendon that it shares with the costal head. This inscription is located in a more or less transverse plane behind the quadrato-mandibular joint. A second, more anterior tendonous inscription was found in approximately one third of the individuals.

The costal head forms the ventral origin of the *M. neurocostomandibularis*. This head arises by a series of narrow slips, each attached to the distal end of an anterior rib. The number of these slips is difficult to ascertain because the more posterior ones interlace with fibers of the *M. costocutaneous inferior*. In *Coluber* the single slips usually are confined to the second through sixth ribs (over half the specimens examined). In some individuals slips also arise from ribs seven and eight; in others they are confined to ribs two to four. The shorter first rib is not a site of attachment. The individual muscle slips are arranged in cranially directed straps. The posterior elements form a single superficial strap overlapping the anterior elements which form a deeper one. The anterior strap inserts on the tendonous inscription deep to the vertebral head. The superficial sheet inserts on the inscription above the deeper strap, although some of its medial fibers pass over the inscription and fuse with the terminal belly that inserts on the mandible.

Insertion of the *M. neurocostomandibularis* on the mandible is by a flat sheet of muscle originating from the tendonous inscription that unites the vertebral and costal heads. The muscle sheet runs cranial along the ventral surface of the neck and gives rise to a broad aponeurotic tendon. The tendon inserts on the ventral surface of the posterior half of the lower jaw.

The *M. neurocostomandibularis* has been described in several ways. In their study of *Elaphe*, Albright and Nelson (1959) treated the vertebral and costal heads as described here, i.e., two parts of a single muscle. Cowan and Hick (1951) described a third head in *Thamnophis*, the pars hyoideus, which I could not identify in *Coluber*. Langebartel (1968) argued that the heads of origin and the insertion portion are separate muscles because each receives different nerve supplies. Haas (1973) considered it one muscle. Whatever the history, the parts of the *M. neurocostomandibularis* are joined to produce a common action.

M. retractor quadrati (Fig. 4): The *M. retractor quadrati* often is listed as a head muscle in studies on snake feeding mechanisms. To call it a head muscle or cervical muscle is not important. After the head and neck are skinned, the origin of the muscle is free and can be seen fanning out from beneath the *M. cervicomandibularis* and crossing over the vertebral head of the *M. neurocostomandibularis*. It originates as fibers attached to the integument caudal to the lateroposterior border of the *M. neurocostomandibularis*. The muscle begins as a truncate bundle of fibers directed anterodorsally. This portion is brief, for the muscle narrows almost immediately as it passes superficial to the *M. neurocostomandibularis* and disappears under the belly of the *M. cervicomandibularis*. Here it gives rise to a well-developed tendon. The tendon continues in the same anterodorsad direction along the medial surface of the quadrate. It inserts on the posterior process of the proximal end of this bone.

Occipito-vertebral muscles.—In *Coluber constrictor* there are four muscles peculiar to the cervical region that insert on the skull. Three of these are dorsal extensors: the *Mm. spinalis capitus*, *semispinalis cervicis*, *obliquus capitus magnus*; and one is a ventral flexor, *M. rectus capitus anterior*. None has been described for snakes although their probable homologues are known in some lizards (e.g., *Iguana*: Evans, 1939; *Ctenosaura*: Oelrich, 1956). In fact, they are named here for the analogous muscles described in these genera. Two of the muscles are large and conspicuous. These are the *M. obliquus capitus magnus* and *M. rectus capitus anterior*. The *Mm. spinalis capitus* and *semispinalis cervicis* are less distinct, but should be considered separately.

M. spinalis capitus (Figs. 5, 8 and 9): As viewed dorsally this is the most anteromedial of the cervical muscles. Medial to it are neural spines of the axis and third and fourth vertebrae. Laterally is

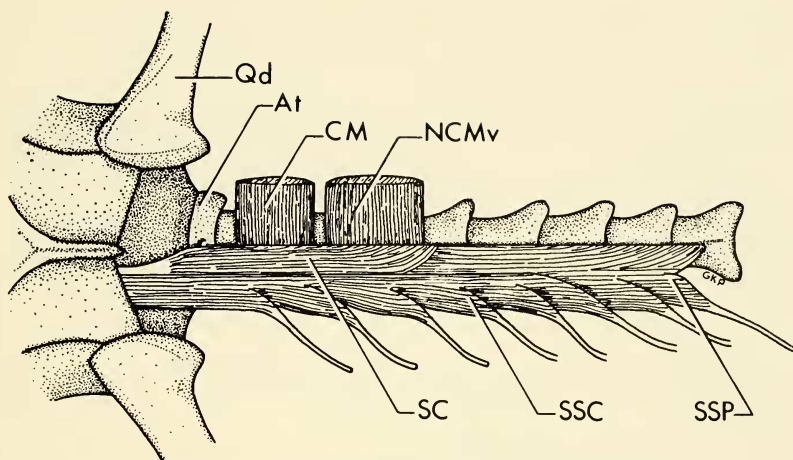


Figure 5. Spinal cervical muscles of *Coluber constrictor*: Dorsal view. M. neurocostomandibularis and M. cervicomandibularis have been cut and deflected dorsally. At, atlas; CM, M. cervicomandibularis; NCMv, M. neurocostomandibularis—vertebral head; Qd, quadrate; SC, M. spinalis capitus; SSC, M. semispinalis cervicus; SSP, M. spinalis-semispinalis.

the M. semispinalis cervicus and deep is the M. obliquus capitus magnus. The muscle could be considered part of the axial spinal muscle M. spinalis-semispinalis. Its origin, however, is unlike any other muscle found in the neck or trunk.

The muscle originates partly as fibers directly from the fascia above the ligamentous sheath enclosing the terminal tendons of the M. spinalis-semispinalis. Most of it arises as small slips attached by very short medial tendons. The tendons are fixed to the posterior-dorsal angle of the neural spines of the axis and third and fourth vertebrae. They are visible only on the ventral surface of the muscle and become progressively thinner caudally. In smaller specimens and juveniles only the axis tendon may be present so that the majority of the muscle arises directly as fibers. The fibers of the small slips fuse and are directed towards the head in a narrow strip terminating in a short tendon. The tendon inserts on the supraoccipital crest.

The muscle is separated laterally from the M. semispinalis cervicus by the terminal tendon of a M. spinalis-semispinalis muscle passing through the fibers to the nuchal ligament. The deeper fibers of the M. spinalis capitus and M. semispinalis cervicus intermingle with each other and are difficult to separate. The result is a muscle whose origin is clear enough, but otherwise difficult to define.

M. semispinalis cervicus (Figs. 5, 8 and 9): The M. semispinalis cervicus essentially is the anterior termination of the M. semispinalis column of the trunk. Its status as a separate muscle could be argued, but because its position and relationship is unique, a different name seems warranted. It lies lateral to the M. spinalis capitus, medial to the M. longissimus dorsi and superficial to the M. obliquus capitus magnus.

The individual slips comprising the muscle arise from the medial tendons of the M. longissimus dorsi. Usually these are the seven most anterior medial tendons of that muscle. However, the number of tendons varies from five to nine. In the trunk, the individual muscles arising from the medial tendons of the M. longissimus dorsi become the Mm. semispinalis, which join with more medial muscle elements (Mm. spinalis) to form the column of the M. spinalis-semispinalis. In the neck region they do not join medial components, but coalesce with each other distally. Separation of the individual slips is possible, but the deeper and more anterior fibers may fuse with the M. spinalis capitus. The entire muscle inserts on the dorsomedial aspect of the exoccipital crest by two or three short tendons.

M. obliquus capitus magnus (Figs. 7-9): This muscle is exposed by removing the M. spinalis capitus and M. semispinalis cervicus and by pulling the M. longissimus dorsolaterally. Its thick fleshy appearance makes it one of the more conspicuous muscles of the neck. It overlies the neural arches of the third vertebra, axis and atlas, and the roof of the foramen magnum. Deep and medial to it are fibers of the M. multifidus.

The muscle originates posteriorly by a weak tendon attached to the dorsal fascia of the fourth vertebra, but most of it arises as fibers from the neural spines of the third vertebra and axis. Near the occiput the muscle becomes thickened laterally and ventrally because the more superficial fibers

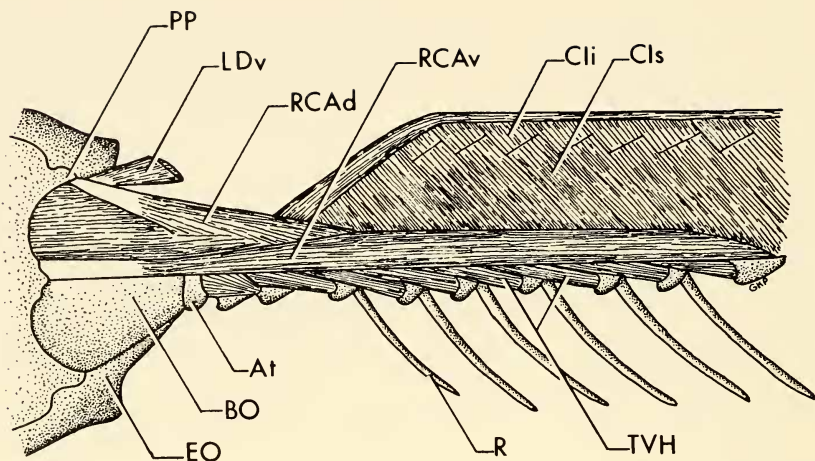


Figure 6. Ventral cervical muscles of *Coluber constrictor*: M. rectus capitus anterior and costal muscles have been removed from the left side to expose the M. transversohypapophyseus. At, atlas; BO, basioccipital; CIi, M. costalis internus inferior; CIs, costalis internus superior; EO, exoccipital; LDv, M. longissimus dorsi—ventral head; PP, paraoccipital process; R, rib; RCAd, M. rectus capitus anterior pars dorsalis; RCAv, M. rectus capitus anterior pars ventralis; TVH, M. transversohypapophyseus.

are bent at almost right angles to the horizontal. In cross section it would appear wedge-shaped. Thus, the muscle is blunt anteriorly but tapered caudally. The ventrolateral edge of the muscle is free, and the muscle can be lifted up and away from the neural arches if the insertion on the exoccipital is cut. However, the deeper medial muscle fibers above the axis do not easily separate from those of the M. multifidus.

The M. obliquus capitus magnus inserts over a wide area of the exoccipital. Dorsally the muscle swings away from the vertebral midline near the atlas and fills most of the depression formed by the roof of the foramen magnum and the crest of the exoccipital bone by a ligamentous connection and a short wide lateral tendon.

M. rectus capitus anterior (Figs. 6, 9 and 10): The muscle forms a long, well-developed column on the ventral surface of the vertebral column from the eleventh vertebra forward to the basioccipital. It is the only subvertebral muscle inserting on the skull and is therefore the primary flexor of the head and neck. A similar muscle was described by Albright and Nelson (1959) as the M. transversohypapophyseus. However, the M. rectus capitus anterior and M. transversohypapophyseus are both present in colubrids and from their description it is not clear as to which muscle they are referring. Apparently they have confused the former with the latter and in doing so did not properly describe either.

The M. rectus capitus anterior has two heads; a pars ventralis and a pars dorsalis. The pars ventralis is the longest and most ventromedial portion of the M. rectus capitus anterior. Lateral to the pars ventralis is the M. costalis internus superior, medial to it are the vertebral hypapophyses, dorsal are the pars dorsalis and M. transversohypapophyseus. Ventral to the pars ventralis is the esophagus. The muscle originates as fibers from the hypapophyses of the eleventh vertebra and those cranial to the axis. In some cases, the anterior muscle fibers arise by short tendons. Fibers from successive hypapophyses intermingle with each other cranially to form a long thick muscle column. The pars ventralis inserts on the prominent median basioccipital process by a long wide tendon. The length of the insertion tendon varies. It may extend caudad (buried deep in the fibers) to the fifth or sixth vertebra, or it may be short and superficial and extend only as far back as the axis. There is also variation in the width of the muscle at its anterior end. In fully adult specimens it is narrow and difficult to separate from the *pars dorsalis*. These individuals have long insertion tendons. In subadults and juveniles the anterior end of the pars ventralis is wide and noticeably overlaps the pars dorsalis. They have short insertion tendons.

The relationship of the pars dorsalis to the pars ventralis is complicated. Fibers from both intermingle near the occiput and cannot be completely separated. Furthermore, the pars dorsalis has two heads; a longer lateral head and a shorter medial head. The lateral head originates from the hypapophyses dorsal to the pars ventralis, but reaches caudally only as far as the fourth vertebra. Its

fibers fuse as they swing laterally away from the pars ventralis. Near the level of the axis (its most anterior origin) the lateral head gives rise to a stout tendon that inserts on the paraoccipital process, ventral to the insertion of the ventral head of the *M. longissimus dorsi*. Thus, it assists in lateral head movement.

The medial head of the pars dorsalis arises in common with the lateral head near the latter's anterior limit, and additionally by a tendon from the basal prominence of the axis intercentrum. The belly of the muscle fans out between the lateral head and the pars ventralis and inserts onto the basioccipital, covering it entirely.

MODIFIED TRUNK MUSCLES IN THE NECK REGION

Axial spinal muscles.—When the superficial cervical muscles have been cut and deflected and the underlying fascia removed, the axial spinal muscles are exposed. Most conspicuous are the three longitudinal columns that extend the length of the trunk. These three muscle columns represent the sacro-spinalis complex of higher vertebrates (Mosaur, 1935). The most medial and dorsal column is the *M. spinalis-semispinalis* complex. The most ventral and lateral column is the *M. retractor costae* biceps and the middle column is the *M. longissimus dorsi*. All three insert on the occiput and have a relationship to one another in the neck different from that of the trunk. In the trunk they are directly connected to one another by lateral and medial tendons of the *M. longissimus* and act as dorsal and lateral flexors of the vertebral column. They are more indirectly connected in the neck region and act as extensors and flexors of the head. The deep axial spinal muscles are the *M. multifidus* and *M. digastricus dorsalis*.

M. spinalis-semispinalis (Figs. 4, 5, 8, 9 and 12): This column of muscles is the most dorsal and medial of the epaxial trunk muscles. It lies against the vertebral neural spines superficial to the fibers of the *M. multifidus*. Lateral and ventral to it is the column of the *M. longissimus*. Mosaur described the repetitive nature of this muscle in the trunk of *Masticophis*. The arrangement in *Coluber* is in agreement.

In the neck region the *M. spinalis-semispinalis* interacts closely with two other muscles that insert on the occiput. These are the *M. spinalis capitus* and *M. semispinalis cervicus*. Their relationships are quite complicated and require an understanding of the trunk musculature to dissect them properly. I will review the *M. spinalis-semispinalis* as it occurs in the trunk and then discuss its termination on the skull.

In the trunk the two parts of the *M. spinalis-semispinalis* are clearly distinct in the Colubridae because the muscle has two heads of origin. The medial head is the *M. spinalis*. It originates as fleshy fibers from the tendons of the *M. multifidus* which lies deep to it. The *M. spinalis* is partly concealed laterally by the long slender tendons that cross it obliquely dorsocranially. The fibers run cranially and slightly laterad for about three segments before fusing with fibers of the lateral head, the *M. semispinalis*.

The lateral head, or *M. semispinalis*, originates from the medial tendon of the *M. longissimus*. This tendon passes cranially for approximately five segments before it gives rise to the spindle-shaped muscle belly of the semispinalis. The muscle belly is directed cranially and somewhat dorsally for another four segments, and then joins the medial head. The common muscle that results continues its course anteriorly for another two to three segments and finally gives rise to a long slender tendon. The tendon passes obliquely cranially and dorsad, crossing superficially to the medial spinalis muscles, and then travels dorsal along the neural spines. Here it is enclosed in a tough, ligamentous sheath along with terminal tendons from other spinalis-semispinalis muscles. The individual tendon finally inserts on the posterior dorsal aspect of a neural spine some 13 to 15 segments anteriorly from the point of origin. Thus the total length of a single muscle is quite long, about 18 to 20 segments. Dissection of the muscle is complicated because (1) there are as many individual muscles as there are trunk segments and (2) each muscle is overlapped caudally by the muscle that immediately precedes it.

In the neck region the *M. spinalis-semispinalis* is modified considerably. The modification is a result of (1) the interlacing of other axial muscles (see *Mm. spinalis capitus*, *semispinalis cervicus*, *multifidus*) and, (2) the necessary shortening of the terminal tendons and muscle fibers to accommodate termination of the muscle column on the skull.

The two heads of the muscle continue to arise as they do in the trunk up to the region of the sixth or seventh vertebrae. It should be apparent that the insertion tendons of individual muscles in the neck cannot run 13 to 15 segments as they do in the trunk. In fact, the most anterior individual muscle with a tendon of this length begins at about the sixteenth vertebra. Muscles originating anterior to this one are not as long, and they have insertion tendons that become progressively shorter, about one half segment length shorter for each segment cranially. Accordingly, the tendon inserting on the axial neural spine is only seven to eight segments in length. The tendon inserting on the axis is the most anterior one to be enclosed in the ligamentous sheath, but there are two other tendons that insert farther forward. The tendon next in sequence does not insert directly on the atlas as expected, but to the nuchal ligament that covers the atlas. This tendon is very thin and passes superficially through fibers of the *M. spinalis capitus* and *M. semispinalis cervicus*; it acts as a shallow

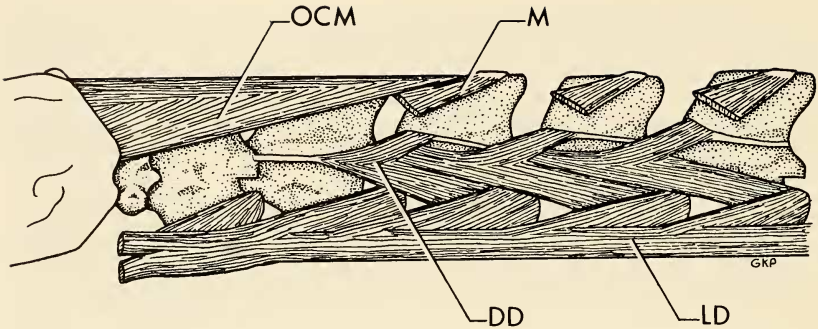


Figure 7. Some deeper cervical muscles of *Coluber constrictor*: Left lateral view. M. longissimus dorsi has been pulled ventrolaterally to expose M. digastricus dorsalis. DD, M. digastricus dorsalis; LD, M. longissimus dorsi; M, M. multifidus; OCM, M. obliquus capitus magnus.

inscription between these two muscles. The tendon is between five and six segments in length. Careful dissection will show that the spinalis portion from which it arises is made up of fibers originating from two or three multifidus muscles instead of one as in the trunk.

One more tendon remains and it represents the most anterior extent of the spinalis-semispinalis muscle column. It inserts on the supraoccipital crest medial to the insertion of the M. spinalis cervicis. The tendon is short, only four or five segments in length, and passes directly through the fibers of the M. semispinalis cervicis. Its association with this muscle is nearly inseparable and the tendon even contains some of its fibers.

The variability of the spinalis-semispinalis muscle in the neck is moderate. The arrangement described is typical of most of the material examined, but the presence of more than one tendon inserting on the supraoccipital crest occurred in several instances, particularly in larger specimens. Also, the coalescence of the two antermost muscles with the M. spinalis capitus and M. semispinalis cervicis is such that it is nearly impossible to clearly distinguish their boundaries. The most important point is that the column does not terminate abruptly on the skull but, instead, it terminates by a short, thin tendon that represents a gradual reduction in fiber and tendon length of the most anterior muscles in the column.

M. longissimus dorsi (Figs. 4 and 6-11): The M. longissimus dorsi is the intermediate column of axial spinal muscles. In the trunk the muscle column arises by as many slips as there are body segments; each slip arises from a short tendon attached to the cranial circumference of a vertebral accessory process. Successive slips overlap one another caudally to form a muscle column ventrolateral to the M. spinalis-semispinalis and dorsomedial to the column of the M. retractor costae biceps. At the anterior end of each slip is an aponeurotic tendon. The tendon bifurcates almost immediately into medial and lateral tendons. The medial tendon courses anteromedial for five segments, passing through the intermuscular septum and gives rise to the lateral head of the M. spinalis-semispinalis. The longer lateral tendon runs anterolaterad for about eight segments and gives rise to the medial head of the M. retractor costae biceps. This is the arrangement of the M. longissimus dorsi throughout the trunk. Individual slips continue to arise as far cranial as the axis. Because there is no accessory process on the axis, this slip is attached to the process of the postzygapophysis, in common with the rudimentary accessory process of the third vertebra.

Modification of the M. longissimus in the neck region begins near the twentieth vertebra. From this point cranial, the individual muscles and their medial and lateral tendons become gradually shorter. At the level of the tenth vertebra the medial tendons are only three or four segments long and the lateral tendons one or two segments. The muscle slips arising anterior to the tenth vertebra no longer terminate in a bifurcate tendon; they fuse with one another at their anterior ends. Slips from the ninth vertebra to the fifth vertebra join those arising from the fourth vertebra to the axis by a tough tendinous inscription which runs obliquely anterodorsad through the muscle column near the level of the third vertebra. The inscription divides the whole column into dorsal and ventral heads; however, the heads are not distinct because the inscription does not pass completely through the fibers. Thus, the M. longissimus actually inserts on the skull by two heads. The dorsal head more or less represents the termination of slips from the fifth through ninth vertebrae and inserts by a short wide tendon onto the narrow lateral angle of the exoccipital crest. The ventral head is formed by fibers from slips originating from the axis to the fourth vertebra. This head runs farther cranially than the dorsal head because it passes ventral to the latter and inserts on the more cranially placed paraoccipital process.

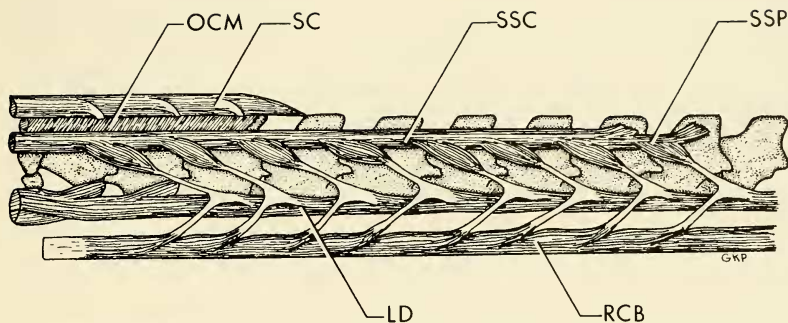


Figure 8. Axial spinal muscles in the neck region of *Coluber constrictor*: Left lateral view. M. longissimus dorsi and M. retractor costae biceps have been pulled ventrolaterally to expose tendons. M. spinalis capitus has been deflected dorsomedial. LD, M. longissimus dorsi; OCM, M. obliquus capitus magnus; RCB, M. retractor costae biceps; SC, M. spinalis capitus; SSC, M. semispinalis cervicis; SSP, M. spinalis-semispinalis.

The anterior structure of the M. longissimus dorsi is further complicated by the presence of the M. retractor costae biceps. The latter closely overlaps the M. longissimus laterally and inserts in common with the ventral head.

M. retractor costae biceps (Figs. 4, 8, 10 and 12): Following the long axis of the trunk laterally is a wide column of muscle, the M. retractor costae biceps. The column lies ventrolateral to the M. longissimus dorsi and dorsomedial to the M. supracostalis lateralis. Mosaur (1935) described the M. retractor costae biceps as a modified ileocostalis muscle and therefore part of the vertebral costal muscle group. The muscle is discussed here because of its close association with the M. longissimus dorsi, particularly in the neck.

In the trunk, the individual slips of the M. retractor costae biceps originate from the lateral tendons of the M. longissimus. Each tendon ends in a thin band of muscle that Mosaur termed the medial belly of the M. retractor costae biceps. The medial belly runs cranial, passing over four ribs, then narrows into a short tendon. The tendon continues anterior and slightly ventrad for another two segments before joining a lateral belly. The lateral belly passes over four more ribs, finally giving rise to a terminal tendon that inserts on a rib shaft some twelve segments anteriorly. The total length of an individual muscle is more than twenty segments, and each is overlapped closely by the caudally adjacent segment. I was not able to separate the medial and lateral bellies from their adjacent counterparts as Mosaur described them, but the tendons connecting the medial and lateral bellies were found easily.

In the neck region the M. retractor costae biceps is best considered in two parts—(1) the insertions of the terminal tendons from the lateral bellies and (2) the termination of the column of muscle fibers (medial and lateral bellies) that arises cranial to the lateral belly that gives rise to the most anterior terminal tendon.

The anterior terminal tendons can be exposed by pulling the ventral side of the muscle column dorsally and away from the body. The tendons are arranged in an overlapping fashion, but each can be separated and followed to its respective rib. All ribs, including the shorter first rib articulating with the fourth vertebra, bear an insertion tendon. Three other tendons insert even farther anteriorly. These attach to the transverse processes of the third vertebra, axis and atlas. As pointed out, the insertion tendons in the trunk are approximately twelve segments in length. However, those that begin anterior to the sixteenth vertebra become gradually shorter so that the tendon inserting on the transverse process of the atlas is only six or seven segments in length. The precise site of this transition in length is variable and may be difficult to determine.

Remaining are the muscle fibers that arise from the lateral tendon of the M. longissimus cranial to that lateral belly the tendon of which inserts on the atlas transverse process. This column is simply a continuation from the trunk and represents a fusion of fibers from individual slips too far anterior to bear terminal tendons. In other words, cranial to the eighth vertebra, the medial and lateral bellies form a single column without insertion tendons. The column becomes very thin near the third vertebra and terminates as an aponeurosis. The aponeurosis is continuous with the tendonous fascia surrounding the ventral head of the M. longissimus dorsi, and thus inserts in common with it on the paracoccipital process.

The attachment of the M. retractor costae biceps to the skull is tenuous and indirect; therefore, the muscle does not function significantly in cranial mobility.

M. multifidus (Figs 7, 11 and 12): This is the deepest of the dorsal spinal muscles. It connects successive vertebrae. It is exposed in the trunk by removing the *M. spinalis-semispinalis* and in the neck by removing the *Mm. spinalis capitus, semispinalis cervicis* and *obliquus capitus magnus*. Throughout the trunk each muscle arises by a tendon from a vertebral neural spine. The muscle is directed obliquely anterolaterad. The deeper fibers insert on the posterior border of the neural arch of the second vertebra, whereas the more superficial fibers insert on the fourth vertebra anterior. This repetitive arrangement continues uninterrupted throughout the trunk. The series inserts most anteriorly on the atlas. No fibers insert on the skull.

In the neck region the *M. multifidus* appears basically as it does in the trunk. Only the two most anterior muscles are modified. They are shorter and their fibers are directed more laterally. The muscle originating from the neural spine of the fourth vertebra mostly passes over the third vertebra and inserts partly on the axis lamina and partly on the atlas. The fibers inserting on the atlas do so mainly by a short tendon attached to the caudal process above the postzygapophysis. The succeeding and most anterior multifidus muscle is peculiar. It originates by a tendon from the axis neural spine. The muscle fibers are directed almost completely in a lateral direction. They cover the neural arch of the axis and insert on the postzygapophysial process of the atlas. Superficial fibers interlace with those of the *M. obliquus capitus magnus* which overlies them.

M. digastricus dorsalis (Figs. 7, 11 and 12): Mosaur (1935) described the complicated arrangement of this muscle in the Colubridae and noted that it probably represents the *M. interarticularis superior* of boids. Gasc (1967) insisted that this was indeed the case and that the muscle is not a digastricus at all, but simply an interarticularis muscle that has lost part of its osseous connection. It is exposed by removing the *M. spinalis-semispinalis* and by pulling the *M. longissimus dorsi* ventrally. It is also of the repetitive type with all the segments together forming a narrow longitudinal muscle column. Individual segments arise by two heads. A medial head, which is covered in part by fibers of the *M. multifidus*, originates by a tendon fixed to the postzygapophysis. A lateral head arises in part by a tendon attached to the accessory process and in part by fibers from a tendonous raphe shared with the medial side of the *M. longissimus dorsi*. The two heads join and extend over three segments to insert by a tendon onto the postzygapophysis of a more cranial vertebra.

The muscle is modified only slightly in the neck region. Beginning from the twelfth to fifteenth vertebrae and continuing cranially, the lateral head arises more from the raphe shared with the *M. longissimus* and less on its own from the accessory process. The most anterior insertion of the *M. digastricus dorsalis* is on the postzygapophysis of the axis.

Subvertebral muscles.—There are two subvertebral muscles—the *M. transversohypapophyseus* and the *M. costovertebrocostalis*. They are intimately associated, and are best understood if dissected concurrently.

M. transversohypapophyseus (Figs. 6, 12): This ventral spinal muscle, peculiar to colubrids, is restricted approximately to the fifty anterior vertebrae in *Coluber constrictor*. In colubrid snakes that have well-developed hypapophyses throughout the trunk, the muscle extends to the vent (Mosaur, 1935). Ventrally it is covered by the aponeurotic origin of the *M. costalis internus superior*, which, if deflected, will expose the tendonous slips of the individual muscles. In the neck, the *M. rectus capitus anterior* must also be removed. The single slips arise by a fleshy connection from the cranial circumference of a transverse process and, as a narrow band of muscle, runs anteriorly for three or four segments and inserts by a tendon onto the posterior angle of a vertebral hypapophysis. The caudal muscles overlap the cranial ones, interlacing as they do so.

In the neck, the *M. transversohypapophyseus* inserts as far cranially as the atlas. I found no evidence of it inserting on the skull, but there are a few peculiarities of the muscle in this area. First, the muscles that originate from the third and fourth vertebrae are shorter than those of the trunk. They insert by a common tendon onto the basal protuberance of the atlas intercentrum. Second, several individuals (6 of 18) showed the curious condition of a second, more lateral tendon inserting on the ventrolateral margin of the axis centrum. Third, there are additional anterior fibers arising from the third vertebra and the axis. Together with two or three tiny tendons, they insert on the dorsal border of the atlas intercentrum. Their arrangement gives a crescent-shaped appearance to this angle of the atlas-axis articulation. I am unsure what muscle these fibers represent. They may be part of the *M. costovertebrocostalis* but they seem associated more closely with the *M. transversohypapophyseus*.

M. costovertebrocostalis (Fig. 11): Exposing this muscle can be a memorable exercise in patience and dexterity. It is small and occupies the intercostal space around the ventrolateral surface of the vertebra, the transverse process and rib heads. Medial to the *M. costovertebrocostalis* is the hypapophysis, lateral is the *M. intercostalis quadrangularis*, dorsal is the *M. tuberculocostalis* and ventral the aponeurosis of the *costalis internus superior* and the *M. transversohypapophyseus*. The muscle originates on the ventrolateral margin of the centrum and runs caudally, inserting on the ventral tubercle of the capitulum costae of the succeeding rib. Mosaur (1935) described two heads to this muscle—a dorsal head joined to a ventral head by a short raphe. In the anterior trunk I could not identify separate heads, only the single muscle. This would support Auffenberg's assumption that

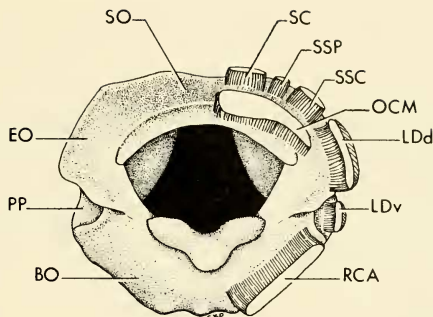


Figure 9. Cranial view of occiput of *Coluber constrictor*: Insertions of occipito-vertebral muscles are shown on the right side. BO, basioccipital; EO, exoccipital; LDd, M. longissimus dorsi—dorsal head; LDv, M. longissimus dorsi—ventral head; OCM, M. obliquus capitis magnus; PP, paraoccipital process; RCA, M. rectus capitis anterior; SC, M. spinalis capitis; SO, supraoccipital; SSC, M. semispinalis cervicis; SSP, M. semispinalis cervicis.

the ventral head of the muscle has been replaced by the M. transversohypapophyseus in those colubrids bearing well-developed hypapophyses (Auffenberg, 1958).

In the neck, this muscle is found anteriorly as far as the fourth vertebra and it inserts on the capitulum costae of the rib articulating with it. It is shorter than its trunk counterparts.

Other vertebral-costal muscles.—Two miscellaneous vertebral-costal muscles are the M. interarticularis inferior intertendinosus and M. levator costae.

M. interarticularis inferior intertendinosus (Figs. 10 and 11): This thin column of muscle is at first difficult to locate because of its proximity to the ventromedial side of the M. longissimus. To expose it, the M. retractor costae biceps must be removed and the M. longissimus dorsi pulled gently dorsad. The individual muscles form a narrow column of intermingling fibers. Each arises from an accessory process, in common with the M. longissimus. The fibers are sent craniad where some of them insert onto succeeding accessory processes. Most of the muscle inserts on the tendon of a levator costae muscle. The deeper fibers insert on the succeeding tendon, but the more superficial ones will reach to the fourth tendon ahead.

In the neck, the main column reaches as far craniad as the accessory process of the third vertebra and the tendon of the most anterior levator costae muscle. Anterior to this insertion, a small segment of the muscle column connects the first three vertebrae. This smaller element originates from the prezygapophysis of the third vertebra and passes craniad where most of its fibers terminate on the neural arch pedicle of the axis. A narrower collection of fibers passes below these and forward into the

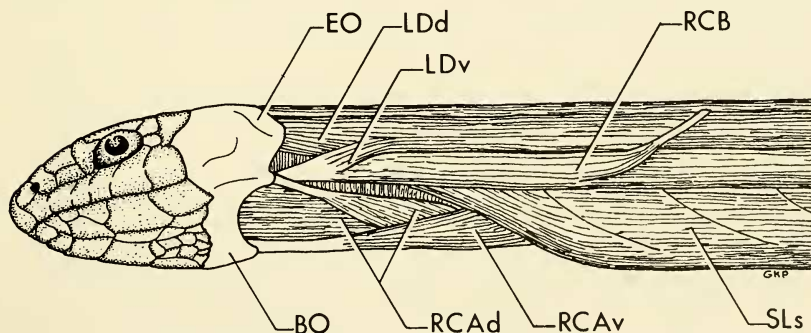


Figure 10. Occipito-vertebral muscles of *Coluber constrictor*: Ventrolateral view. Note insertion of M. retractor costae biceps in common with ventral head of M. longissimus dorsi. BO, basioccipital; EO, exoccipital; LDd, M. longissimus dorsi—dorsal head; LDv, M. longissimus dorsi—ventral head; RCAd, M. rectus capitis anterior pars dorsalis; RCAv, M. rectus capitis anterior pars ventralis; RCB, M. retractor costae biceps; SLs, M. supracostalis lateralis superior.

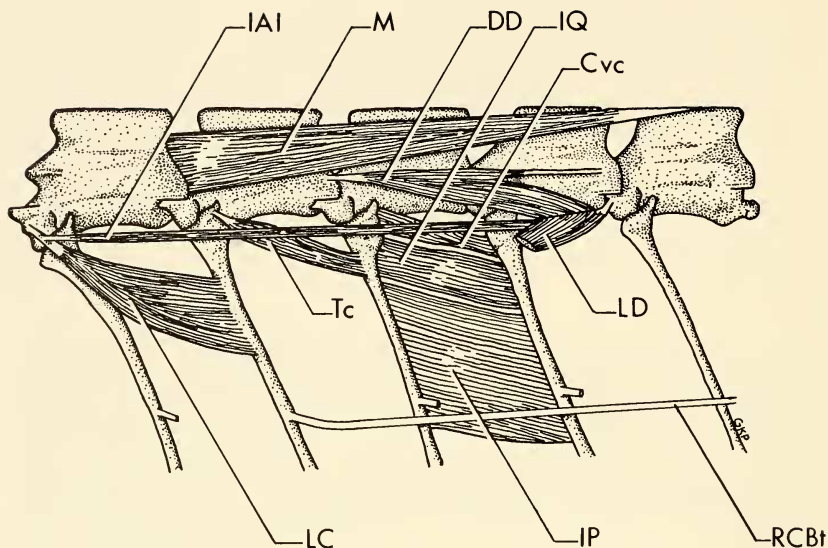


Figure 11. Deep muscles of the trunk and neck of *Coluber constrictor*: Lateral view (modified from Gasc, 1967). Cvc, M. costovertebrocostalis; DD, M. digastricus dorsalis; IAI, M. interarticularis inferior intertendinosus; IP, M. intercostalis proprius; IQ, M. intercostalis quadrangularis; LC, M. levator costae; LD, M. longissimus dorsi; M, M. multifidus; RCBt, terminal tendon of M. retractor costae biceps; Tc, M. tuberculocostalis.

posterolateral wall of the atlas neural arch.

M. levator costae (Fig. 11): The belly of this muscle is exposed by pulling the column of the *M. retractor costae* dorsally and medially. Its tendinous origin remains concealed by the column of the *M. interarticularis inferior intertendinosus*, which covers it laterally. The muscle is more or less diamond-shaped and occupies the vertebral portion of the intercostal space lateral to the *M. tuberculocostalis*. Its origin is by a strong tendon arising from the caudal circumference of the accessory process. The tendon crosses over the rib articulating with the same vertebra and passes into the muscle fibers. The fibers are directed caudally and ventrally, following the lateral body contour. They insert on the cranial border of the adjacent caudal rib shaft near the insertion of the terminal tendon of the *M. retractor costae* biceps.

The *M. levator costae* is attached to all of the ribs in the neck region. There is slight but noticeable modification of the muscle acting on the first rib. It is the most anterior levator costae muscle and arises from the diminutive accessory process of the third vertebra. The muscle belly is shorter and narrower than those of the trunk and adheres closely to the terminal bundle of the costal muscles on its cranial side. Its deeper fibers insert on the shaft of the first rib, whereas the superficial fibers pass over it and join those from the same muscle that insert on the second rib.

COSTAL MUSCLES

The costal muscles will be considered in two groups. The first group includes two muscles occupying the intercostal space on the upper one-third of the rib shafts. These are the *M. tuberculocostalis* and *M. intercostalis quadrangularis*. Their close association with neighboring vertebral-costal muscles (*Mm. levator costae*, *costovertebrocostalis*) warrants brief but separate descriptions of each.

The second group includes the other costal muscles. They are found on the lower two-thirds of the rib shafts forming a fleshy stratum that (1) connects successive ribs and (2) forms throughout the trunk a covering on the inner and outer surfaces of the ribs. These muscles are the *Mm. intercostalis proprius*, *supracostalis lateralis superior* and *inferior*, and *costalis internus superior* and *inferior*. Their relationships will be summarized in a single description.

M. tuberculocostalis (Fig. 11): Lying just beneath the *M. levator costae* is a small, somewhat cylindrical muscle, the *M. tuberculocostalis*. Its origin is by a short tendon attached to the caudal circumference of the dorsal rib tubercle. Fibers run obliquely laterad and caudad to insert on the

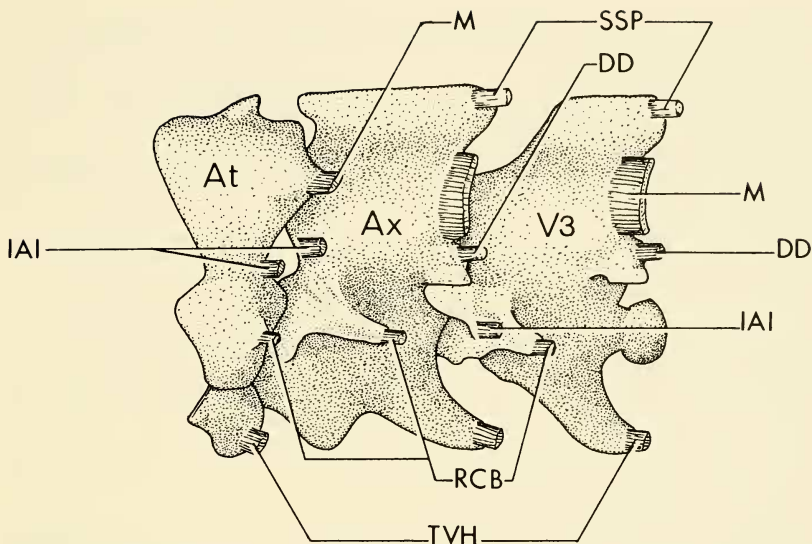


Figure 12. Most anterior three vertebrae of *Coluber constrictor* showing muscle insertions: Left lateral view. At, atlas; Ax, axis; DD, M. digastricus dorsalis; IAI, M. interarticularis inferior intertendinosus; M, M. multifidus; RCB, M. retractor costae biceps; SSP, M. spinalis-semispinalis; TVH, M. transversohypapophyseus; V3, third vertebra.

cranial border of the following rib shaft just below the neck.

The muscle is found anteriorly as far as the intercostal space between the first and second rib.

M. intercostalis quadrangularis (Fig. 11): This is a ventral median costal muscle that lies just lateral to the *M. costovertebrocostalis*. It arises from the medial surface of the ventral tubercle of the rib and passes caudad and laterad to insert on the anterior surface of the succeeding rib. The longer fibers of the muscle are directed at an oblique angle ventrally, thereby giving the muscle a quadrangular shape.

The muscle is found anteriorly as far as the intercostal space between the first and second rib.

Other costal muscles (Figs. 4, 6, 10-12): The remaining costal muscles are the *Mm. intercostalis proprius*, *supracostalis lateralis superior* and *inferior*, and *costalis internus superior* and *inferior*. The *M. intercostalis proprius* is a wide, single muscle sheet that connects successive ribs, filling the ventral two-thirds of the intercostal space. Fibers pass from the posterior border of one rib and insert on the cranial surface of the succeeding caudal rib. The muscle begins in the neck region from the first rib.

Along the trunk, on the lateral and medial surfaces of the ribs, are the *Mm. supracostalis lateralis superior* and *inferior*, and *costalis internus superior* and *inferior*. Both pairs of muscles form a fleshy covering on the outer and inner surfaces of the ribs that, in effect, envelopes the *M. intercostalis proprius*.

Segments of the *M. supracostalis lateralis superior* and *inferior* arise from the lateral surface of each rib. The muscle fibers run caudad, spanning up to fifteen ribs before inserting on the cranial circumference of a rib shaft. Fibers from successive segments interlace with each other, obscuring the origins.

Segments of the *M. costalis internus superior* arise from an aponeurosis attached to the hypapophysis of the vertebrae. Together the segments form a muscle of considerable thickness, which runs at an oblique angle downward and cranial. The separate elements insert on the fifth rib ahead, caudal to the origin of the *M. costalis internus inferior*. The inferior portion is essentially a ventral continuation of the superior, although its segments span only three ribs.

In the cervical region the *M. supracostalis lateralis* and *M. costalis internus* have a unique relationship. They wrap around the cranial surface of the first rib and join each other in a fleshy bundle. This bundle runs obliquely anterodorsad, parallel to the first rib, and narrows into a wide tendon. The tendon inserts on the transverse process of the atlas.

MISCELLANEOUS MUSCLES

Several axial muscles found during the dissection, but not relevant to the study, are mentioned here for the sake of completeness.

Mm. costocutanei superiores et inferiores: These two muscles are the principal elements causing movement between the trunk and the skin. They have been described thoroughly in snakes by Buffa (1904) and Mosaur (1935) and are summarized briefly here.

The individual slips of the *M. costocutaneous superior* (Fig. 4) arise from the lateral side of the ribs and pass outward between the *M. retractor costae biceps* and *M. supracostalis lateralis superior*. The fibers form flat bundles directed backward and laterad. They insert on the lateral and ventrolateral scale rows.

The segments of the *M. costocutaneous inferior* are similar to the *M. costocutaneous superior*. They are attached to the cartilagenous rib tips, run caudad and insert on the sides of the ventral scales and the first three or four scale rows.

Both of these muscles reach the cervical region where they maintain a close alliance with the hyoid and its associated muscles (see Langebartel, 1968 for a full description of hyoid musculature).

Mm. obliquus abdominis internus, transversus abdominis: These two muscles form a double-layered sheet across the ventral aspect of the trunk. The *M. transversus abdominis* lies deep to the *M. obliquus abdominis internus*. Muscle fibers of the former arise from the medial surface of the ribs near their distal ends. They constitute a thin sheet that extends posteriad and mediad to the linea alba. The latter muscle arises and inserts in common with the *M. transversus abdominis*, but its fibers are directed cranial. The two sheets terminate anteriorly at the hyoid cornu.

M. rectus abdominis: This muscle stretches between successive rib cartilages and follows exactly the long axis of the body. It is not particularly distinct from the *M. intercostalis proprius* and some of its fibers even mingle with those of the *M. supracostalis lateralis inferior*.

Connective tissue and fascia.—In *Coluber* there is a well-developed system of intermuscular fascia that furnishes structural and functional stability to the intricate muscle architecture. The formation of fascial tunnels through which the long muscles extend solves numerous packaging problems that result when the muscles are flexed and the body bends and curves. Such tunnels enclose the muscle columns of the axial spinal series throughout the trunk and neck. The fascia surrounding the column of the *M. spinalis-semispinalis* is particularly tough. Medially and dorsally this fascia is continuous with the ligamentous sheath enclosing the terminal tendons of that muscle. Additional fibrous connective tissue stretches the length of the trunk along the dorsal midline above the ligamentous sheath. It connects both *M. spinalis-semispinalis* columns on either side of the neural spines.

A ventral fascia also covers the subvertebral muscles and provides a membrane for the inner body wall.

Other important connective tissue separates the columns of the *M. longissimus* and *M. spinalis-semispinalis* as a *septum intermusculare dorsi mediale* (Mosaur, 1935). The septum is formed from the medial tendons of the *M. longissimus* that pass through it and by the fascia that connects these tendons in a vertical plane (Type A of Mosaur). In some colubrid snakes like *Lampropeltis*, *Rhinocheilus* and *Drymarchon* the medial tendons of the *M. longissimus* fuse with the septum (Type B of Mosaur) and do not pass through to the *M. semispinalis* (see section on Neck Muscles in Other Colubrid Snakes for more detail).

Finally, a *ligamentum nuchae* (nuchal ligament) is present in *Coluber*, though I found no mention of it elsewhere for snakes. The structure appears as a thick fibrous sheet separating the *spinalis capitus* muscles anteriorly on either side of the dorsal midline. The nuchal ligament arises from the midsagittal crest of the supraoccipital bone and reaches posteriorly between these muscles covering the atlas neural arch. It attaches deeply to the neural spine of the axis, but superficially the ligament continues caudad with the dorsal fascia of the neck.

NECK MUSCLES IN OTHER COLUBRID SNAKES

The description of *Coluber* is more meaningful if its range of morphological variation encompasses that found in related genera. Mosaur (1935) concluded that the trunk muscles of most colubrid snakes have an arrangement referable to that of *Masticophis*. From an admittedly small sampling I conclude similarly—most colubrid snakes have cervical muscles similar to those of *Coluber*.

The following genera selected for comparison were placed in the Colubridae by Underwood (1967b). Three are medium sized terrestrial forms: *Lampropeltis getulus californiae* (Blainville), *Elaphe g. guttata* (Linné) and *Pituophis melanoleucus annectens* (Baird and Girard). Another is the large terrestrial snake *Drymarchon corais erebennus* (Cope). The small desert species *Chionactis occipitalis annulata* (Baird) provides a contrast to these generalized types by its commitment to a subterranean existence (see Norris and Kavanau, 1966). The common garter snake *Thamnophis sirtalis* (Linné), placed by Underwood (1967b) in the closely related family Natricidae, was examined for intrafamilial similarity.

The muscles described for *Coluber constrictor* are present in the above snakes with the exception

of the *M. constrictor coli* in *Pituophis* and *Chionactis*. Variation in most muscles is unremarkable and involves minor differences such as the appearance of additional tendons or the interlacing of adjacent muscles. The more obvious are discussed below according to muscle or muscle group.

Dorsal cervical muscles: The *M. spinalis capitis* and *M. semispinalis cervicis* are the most variable muscles, mainly because of the intermuscular septum. Recall that the septum divides the column of the *M. spinalis-semispinalis* from the column of the *M. longissimus dorsi* and receives the medial tendons of the latter muscle. The tendons either pass directly through the septum to the belly of the *Mm. semispinalis* (Type A of Mosaur), or they fuse with the septum, and the belly of the *Mm. semispinalis* arises independently from the medial surface of the septum (Type B of Mosaur). *Coluber*, *Elaphe*, *Pituophis* and *Thamnophis* are Type A. *Drymarchon*, *Lampropeltis* and *Chionactis* are Type B. In the neck of Type A snakes the *M. semispinalis cervicis* arises as it does in *Coluber*. In the neck of Type B snakes the *M. semispinalis cervicis* originates from the medial surface of the intermuscular septum as a bundle of fibers continuous to the anterior limit of the septum. The septum reaches cranially to the fourth or fifth vertebra. The individual slips of the muscle are less distinct in these genera than in the Type A snakes. It would seem that the origin of the muscle by a well-defined tendon is probably the more advanced condition.

There is also modification in the *M. spinalis capitis*. In each genus it originates from the dorsal fascia above the ligamentous sheath enclosing the terminal tendons of the *Mm. spinalis-semispinalis*. In *Coluber* and *Thamnophis* this is by tendonous slips attached to the neural spines, but in *Elaphe*, *Drymarchon* and *Pituophis* only a single tendon arising from the axis neural spine is present. The rest of the origin is fibrous. In these snakes, particularly *Pituophis*, the muscle is wider and quite difficult to separate from the *M. semispinalis cervicis* lateral to it. Interestingly both these muscles are better developed in *Chionactis*. In fact, the axial muscles throughout the trunk of this snake are exaggerated.

M. rectus capitis anterior: This muscle is present in each genus as a *pars ventralis* and a *pars dorsalis*. The two parts are best exhibited in *Drymarchon*, *Pituophis* and *Lampropeltis*. They partly coalesce anteriorly in *Coluber*, *Thamnophis* and *Elaphe* and are almost inseparable in *Chionactis*. There is little difference in the *pars dorsalis*, but in *Elaphe* and *Drymarchon* there is a second tendon from the lateral head of the muscle that inserts just caudal to the one inserting on the paraoccipital process of the skull.

Slips of the *pars ventralis* of *Drymarchon* originate by conspicuous tendons. In the other snakes the slips have a fibrous origin. The *pars ventralis* of *Chionactis* deviates by reaching posteriorly to the eighteenth vertebra, whereas in the other genera the extent of the muscle is invariably restricted to the eleventh or twelfth vertebra.

M. longissimus dorsi* and *M. retractor costae biceps: *Coluber* is unique in that the column of the *M. retractor costae biceps* terminates cranially as an aponeurosis continuous with the fascia surrounding the ventral head of the *M. longissimus*. This connection is fleshy in the other genera and conceals the dorsal/ventral division of the *M. longissimus*. The bulk of the muscle inserting on the paraoccipital process in these snakes is from the *M. retractor costae biceps*. The ventral head of the *M. longissimus* is still present, but it is not as distinct as it is in *Coluber*. For *Elaphe*, *Drymarchon* and *Pituophis* the most anterior medial tendon of the *M. longissimus* passes through the muscle column and completes the division. This tendon inserts on the postzygapophyseal process of the atlas.

M. constrictor coli: This muscle is present in each genus with the exceptions of *Pituophis* and *Chionactis*. However, its apparent absence in them may be a technical artifact. Only one poorly preserved specimen of *Pituophis* was dissected. Although the condition of most muscles was reasonably diagnostic, the *M. constrictor coli* may have deteriorated. *Chionactis*, on the other hand, is such a small snake that the muscle could have been overlooked. In the other genera the muscle is as described for *Coluber*.

Fascia: The intermuscular connective tissue is abundant but irregularly distributed. This is worth mentioning because where there is less connective tissue dissection of muscles is considerably easier. Of course, there may be a functional significance worth exploring because the fascia provides mechanical support. The dorsal fascia is thick and fibrous in *Pituophis*, *Drymarchon* and *Lampropeltis*. It is thinnest in *Coluber* and *Thamnophis*.

Summary of Generic Comparison: Examination of additional colubrid genera supports the conclusion that *Coluber* is typical of the family. The following conclusions apply to the neck muscles in the group as a whole.

1. The myology of the neck region in generalized colubrid snakes approximates that found in *Coluber constrictor*. Variation is limited largely to fiber bulk, number of tendonous origins and fibrous association with adjacent muscles.

2. Of the species compared, *Thamnophis* is the most similar to *Coluber*. I consider the familial ranking of the Natricidae questionable. Underwood (1967b) distinguishes the Colubridae from the Natricidae essentially on hemipenial characters. His classification is used here for the sake of consistency to this presentation and to underscore the prevalence of a *Coluber*-like myology among higher, non-venomous snakes.

3. The myology of *Chionactis* is the most aberrant of the species compared. It has a long M. rectus capitus anterior and a general bulkiness about the axial musculature which seem related to the species burrowing habits.

4. The value of cervical myology as a taxonomic tool at the subfamily and generic level remains to be tested. Currently it appears weakened by the remarkable similarity of muscles found in genera showing diverse life styles and which are taxonomically distinct on other grounds. The muscle architecture of colubrid snakes represents a persistence of common features found throughout the family.

DISCUSSION

When the shoulder girdle was lost in snakes so was the thoraco-cervical boundary, and evidently the body musculature has obliterated any trace of its former position. The anterior trunk muscles are of no help in delimiting the cervical region because each is modified so subtly. For example, muscles associated with the first rib bear nearly the same relationship to each other as they do in the trunk. Moreover, modification of some muscle groups is inconsistent with others. The long muscles (Mm. spinalis-semispinalis, longissimus dorsi, retractor costae biceps) become shorter anteriorly in a graduated sequence, but some of the briefer intervertebral series (Mm. digastricus dorsalis, interarticularis intertendinosus) tend to lengthen. Also, all but two of the occipito-vertebral muscles are continuous with the trunk (Table 1). Thus the terms M. spinalis capitus and M. semispinalis cervicus are at present more convenient than real. One is left with the impression that modification of the trunk musculature in the cervical region reflects accommodation to structural uniformity. Fortunately there are two muscles that prove a neck exists at all. The M. obliquus capitus magnus and M. rectus capitus anterior have no trunk counterparts and they function exclusively for movement of the head and neck. These muscles have probably been retained from a tetrapod ancestry, but I am uncertain as to how they have been modified.

This study of *Coluber* provides several points relevant to understanding the structural evolution of the cervical region in snakes.

1. The skeleton tells us little about the structural history, other than there was intense selective pressure for consistent design.

2. Dissection of adults and juveniles suggests that during ontogeny size increase imposes mechanical demands on the muscles in the form of an increase in the number of tendonous origins and proportionately longer muscles. There is also a corresponding enlargement of the crests and processes of the occipital bones and vertebrae, which should be taken into account by investigators attempting identification of snake vertebrae by statistical analysis.

3. The muscle architecture of colubrids is conservative yet amazingly adaptable, being suitable for sand burrowing as shown by *Chionactis* and perhaps for climbing as well, as in the arboreal colubrids (e.g., *Chrysopelea* or *Oxybelis*) which depend on body rigidity rather than short radius arcs in locomotion (Auffenberg, 1962).

4. Moderate interspecific variation in muscle patterns is tolerable so long as functional units are maintained.

5. The origin of the M. rectus capitus anterior in snakes lacking hypapophyses is unknown. Vertebral hypapophyses are a classic systematic character in snakes, but one which has been difficult to apply. They are varyingly present in both primitive and advanced species (Malnate, 1972). Perhaps correlation with this muscle will help clarify the meaning of the character.

6. Muscles of the neck region can be organized into three groups: (1) those inserting on the occiput that originate anterior to the twelfth vertebra, (2) those inserting on the occiput as a termination of repetitive elements from the trunk, and (3) those muscles continuous with the trunk that do not insert on the occiput, but terminate on the atlas, axis or third vertebra. The most well-defined cervical

muscles are the *M. obliquus capitus magnus* and *M. rectus capitus anterior*. They are restricted to the neck and are probably homologous to the same named muscles described for *Iguana* by Evans (1939) and *Ctenosaura* by Oelrich (1956).

7. The description of *Coluber* is representative of most snakes in the family Colubridae, but the myology may vary slightly in species with special adaptive requirements. Variation of muscle relationships in a species is minor and attributable to ontogenetic change and individual variance.

The functional properties of the neck are more difficult to assess. Because efficient lateral undulatory locomotion is a primary concern of snakes (and indeed a major reason for their success), synchronous and uninterrupted flexion are best accomplished by the head and neck acting functionally as one. Movement at the occipito-vertebral joint is probably more important for feeding and defensive action than for routine cruising and the articulation is typical of most squamates in that versatility is nearly restricted to vertical movement. In colubrids other uses of the head and neck (such as for burrowing) are behavioral adaptations in which any structural modifications are secondarily acquired—for example, the longer *M. rectus capitus anterior pars ventralis* of *Chionactis*.

Further research into the neck morphology of snakes and its relationship to that of other limbless reptiles may help clarify functional properties. The problem is to determine the morphological events in cervical evolution that accompanied limb reduction and loss of the shoulder girdle. The current theory on snake origins states that snakes were derived from limbless or nearly limbless burrowing lizards and that "proto-snakes" subsequently emerged from below ground and diversified (Bellairs and Underwood, 1951; Underwood, 1967b). Logically the next step would be to examine snakes having musculature that is less complicated than the Colubridae, for example boids. Ultimately lizards must be investigated. The published accounts on the myology of limbless species are few and mostly concerned with head musculature; description of body morphology has been generally neglected. In light of the numerous studies on reptilian head morphology (see Gans and Parsons, 1973) it is unfortunate that so many of these ignored the neck region.

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